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**STUDIES ON PALEOCENE AND EARLY EOCENE
APATEMYIDAE (MAMMALIA, INSECTIVORA)**

I. DENTITION OF CLARKFORKIAN *LABIDOLEMUR KAYI*

BY

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**II. *LABIDOLEMUR* AND *APATEMYS* FROM
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WYOMING**

BY

PHILIP D. GINGERICH



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DENTITION OF CLARKFORKIAN *LABIDOLEMUR KAYI*

BY

PHILIP D. GINGERICH¹ AND KENNETH D. ROSE²

Abstract.—New specimens of Clarkforkian *Labidolemur kayi* permit reconstruction of the complete upper and lower dentition of this species, making *Labidolemur* one of the best known genera of early Cenozoic Apatemyidae. *Labidolemur kayi* has a dental formula of $\frac{2.0}{1} \frac{2.2}{0} \frac{3.3}{3}$. It is further characterized by the presence of two enlarged upper incisors, two upper premolars (P² and P⁴), and a long and narrow M¹ with a reduced styler shelf. In the lower dentition, *L. kayi* has a single enlarged lower incisor, three lower premolars (including a very small P₃), and M₃ with a short talonid.

INTRODUCTION

Apatemyidae are an unusual family of extinct insectivorous mammals known from the early or middle Paleocene through early Oligocene of North America and the late Paleocene(?) through late Eocene or early Oligocene of Europe. Some sixteen North American species and thirteen European species of apatemyids have been described, most of which are based on fragmentary material. Apatemyids are known from many fossil localities, but they are always rare faunal elements and few localities contain specimens representing more than one or two individuals. Consequently, the morphology and morphological variability of Apatemyidae are poorly understood, and there is little agreement regarding the systematic relationships of apatemyid genera and species. The purpose of this paper is to describe several unusually well preserved specimens of the late Paleocene and early Eocene species *Labidolemur kayi*.

The following museum acronyms are used in the text and figures: CM (Carnegie Museum of Natural History, Pittsburgh) and UM (University of Michigan Museum of Paleontology, Ann Arbor). Dental nomenclature follows Van Valen (1966) and Gingerich (1976, pp. 5–6, 76–77). Numbered fossil localities prefaced by SC are from the Sand Coulee area of the Clark's Fork Basin, Wyoming. Mammalian faunas of the Clarkforkian Land-Mammal Age are described in a general review by Rose (1981).

NEW SPECIMENS OF *LABIDOLEMUR KAYI*

Several specimens of *Labidolemur kayi*, including left and right dentaries and a right maxilla, were collected by G. F. Gunnell on July 2, 1979, from a small quarry, "Holly's Microsite", at

¹Museum of Paleontology, University of Michigan, Ann Arbor, MI 48109

²Department of Cell Biology and Anatomy, Johns Hopkins University, Baltimore, MD 21205

locality SC-188 in middle Clarkforkian beds of the Clark's Fork Basin in northwestern Wyoming (see Rose, 1981, for discussion of this locality). The next time this quarry was worked, several days later, a right premaxilla of *Labidolemur* was found. None of the specimens were found in articulation and each has been given a separate number (UM 73496, 73500, 73501, and 73616), but the specimens may represent a single individual animal. All four specimens were found in one area of the quarry, and all exhibit the same slight dental wear. Every tooth in the dentition is represented by an intact crown on either the left or right side except I² (damaged), M³ (missing), and P₄ (missing), and no teeth are duplicated.

The right premaxilla of *Labidolemur kayi* from SC-188, UM 73616, is illustrated in Text-figure 1A,B. It includes two teeth with enlarged crowns, which are identified as I¹ and I². The crown of I¹ has a large, simple, pointed anterior cusp (anterocone) and a smaller posterior cusp (posterocone) and is very similar to a specimen from Bear Creek illustrated by Simpson (1928, fig. 12A). In form, the crown of I¹ is also very similar to that of primitive microsypids (Gingerich, 1976, fig. 38). The crown of I² in UM 73616 is partially broken, but this tooth is preserved intact following I¹ in a specimen of *Labidolemur serus* (Gingerich, 1982, fig. 2). In *L. serus* there is a single principal cusp with a distinctively squared lateral profile. Both I¹ and I² in the upper dentition appear to have occluded with I₁ in the lower dentition, the principal cusp of I² opposing distinct denticles on the margocristid of I₁.

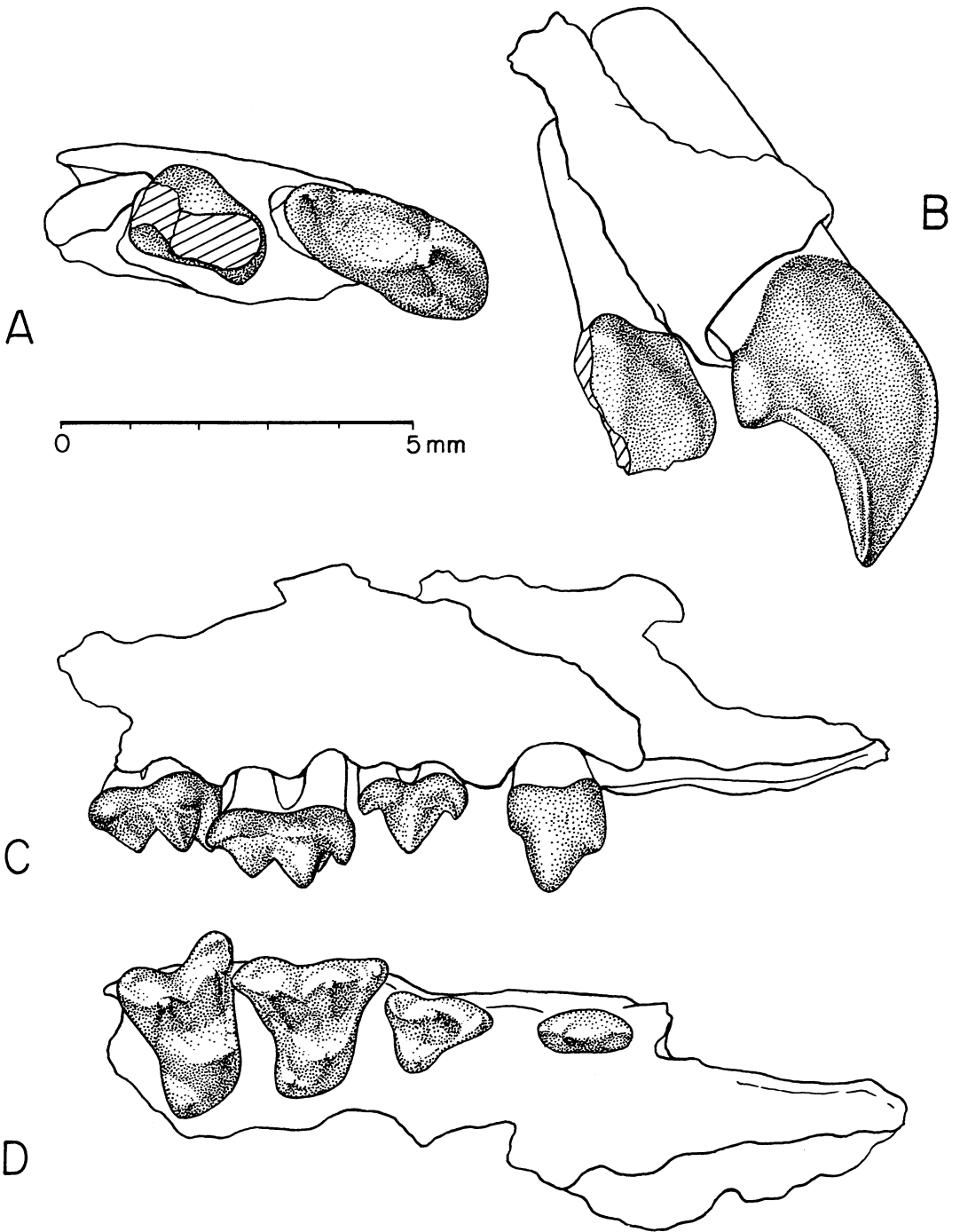
The right maxilla of *Labidolemur kayi* from SC-188, UM 73496, is illustrated in Text-figure 1C, D. Four of an original five cheek teeth are present; only M³ is missing. The most anterior tooth has a long, triangular crown, and it is identified as P² on the basis of its specialized occlusal relationship with P₂ in the lower dentition. There is a small diastema following P², which corresponds to the position of vestigial P₃ in the lower dentition. P⁴ is a relatively simple tooth, with a large labial cusp (paracone), small anterior and posterior styler cusps, and a small but distinct lingual cusp (protocone).

The first upper molar, M¹, has a prominent protocone, paracone, and metacone, with a smaller distinct hypocone and a small parastyle. There are no conules. The styler shelf is narrow, and the parastyle is directly anterior to the paracone. M² in UM 73496 is similar to M¹, but it is a shorter, broader tooth, with the parastyle labial to the paracone and a distinct ectoflexus. Measurements of the upper teeth of *Labidolemur kayi* are listed in Table 1.

The mandibular dentition of *Labidolemur kayi* is illustrated in Text-figure 2, based on UM 73500 and 73501 from SC-188. There is a single lower incisor, I₁, with a long curving crown terminating in a sharply pointed tip. The margocristid on I₁ bears two faint cuspules near the base of the crown. As indicated above, these cuspules oppose the tip of I² in the upper dentition. A similar tooth from Bear Creek was illustrated by Simpson (1928, fig. 14).

P₂ has a distinctively hooked, wedge-shaped crown, which is characteristic of most species of apatemyids. Most of the crown projects in front of the single root, overhanging the base of I₁. P₃ is a very small tooth separated by a short diastema from P₂. It has a simple conical crown measuring 0.3 mm in diameter. The crown of P₄ is missing in UM 73500 but, judging from the holotype of *L. kayi*, this tooth had a simple blunt crown with a rounded protoconid and a small keeled talonid. The alveolus for P₄ is bilobed, suggesting that the two roots of this tooth were solidly fused for most or all of their length.

The three lower molars are all very similar in size and shape. Each has a distinct protoconid and metaconid, with a smaller paraconid. The preprotocristid makes a sharp right angle at the front of the trigonid before joining the paracristid. There is a prominent hypoconid on all three molars, but the rest of the shallowly basined talonid is enclosed by a curving marginal crest. M₁ is distinctive in having a relatively narrower trigonid than the other lower molars. M₂ is distinctive in having a relatively broader trigonid, and M₃ is distinctive in having a relatively



TEXT-FIG. 1 — Upper dentition of *Labidolemur kayi* Simpson from Holly's Microsite (SC-188). Right premaxilla with I¹⁻², UM 73616, in occlusal (A) and lateral view (B). Right maxilla, UM 73496, in lateral (C) and occlusal view (D).

TABLE 1 — Measurements of the upper and lower teeth of *Labidolemur kayi* from Holly's Microsite (SC-188) in the Clark's Fork Basin, Wyoming. L = mesiodistal crown length, W = buccolingual crown width, H = crown height measured at or from the base of the crown. All measurements in mm. Asterisks indicate estimates.

Maxillary dentition (UM 73496, 73616)			Mandibular dentition (UM 73500, 73501)		
I ¹	L	3.1	I ₁	L	6.0
	W	1.4		W	1.7
	H	4.1		H	2.5
I ²	L	2.3*	I ₂	L	—
	W	1.1*		W	—
P ²	L	1.4	P ₂	L	2.3
	W	0.6		W	1.0
P ³	L	—	P ₃	L	0.3
	W	—		W	0.3
P ⁴	L	1.6	P ₄	L	—
	W	1.2		W	—
M ¹	L	2.1	M ₁	L	1.9
	W	2.0		W	1.3
M ²	L	1.9	M ₂	L	1.9
	W	2.5		W	1.5*
M ³	L	—	M ₃	L	1.9
	W	—		W	1.3

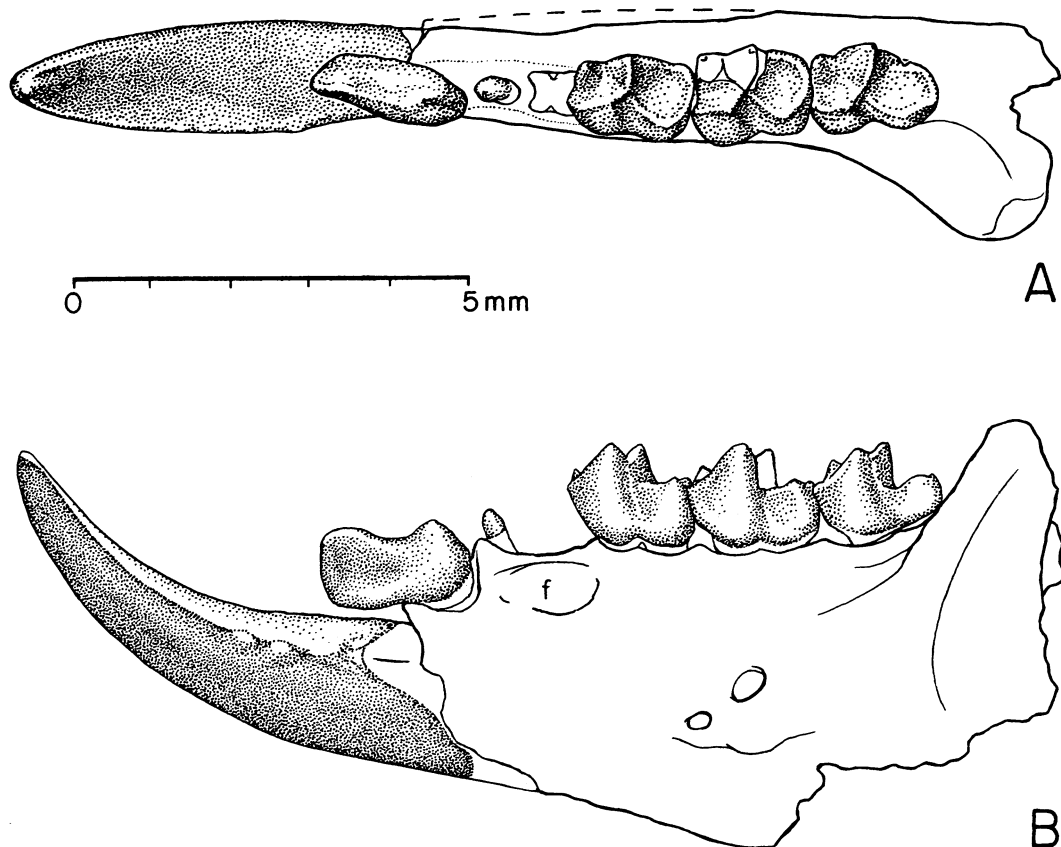
longer and narrower talonid. Measurements of the lower teeth of *Labidolemur kayi* are listed in Table 1.

There is a distinct depression or fossa on the labial side of the dentary below the position of P₄. This depression is well developed in most specimens of *Labidolemur*, and it may have been the site of a gland of undetermined function (West, 1973). Two large mental foramina are also present on the labial side of the dentary below M₁ and M₂. Mandibular depth cannot be measured in UM 73500, but it is 4.9 mm below M₁ in the right mandibular ramus UM 73501.

DISCUSSION

The new specimens of *Labidolemur kayi* described here provide the first indication of the full dental formula in *Labidolemur*. The complete dentition is illustrated in the composite reconstruction shown in Text-figure 3. We interpret the dental formula of *Labidolemur kayi* to be $\frac{2.0}{1.0} \frac{2.3}{3.3}$, and the homologies to be I^{1,2}, P^{2,4}, and M^{1,2,3} in the upper dentition and I₁, P_{2,3,4}, and M_{1,2,3} in the lower dentition. P₃ is much reduced in size in comparison to P₂ and P₄, and, judging from occlusal relationships, its counterpart in the maxilla (P³) was lost entirely.

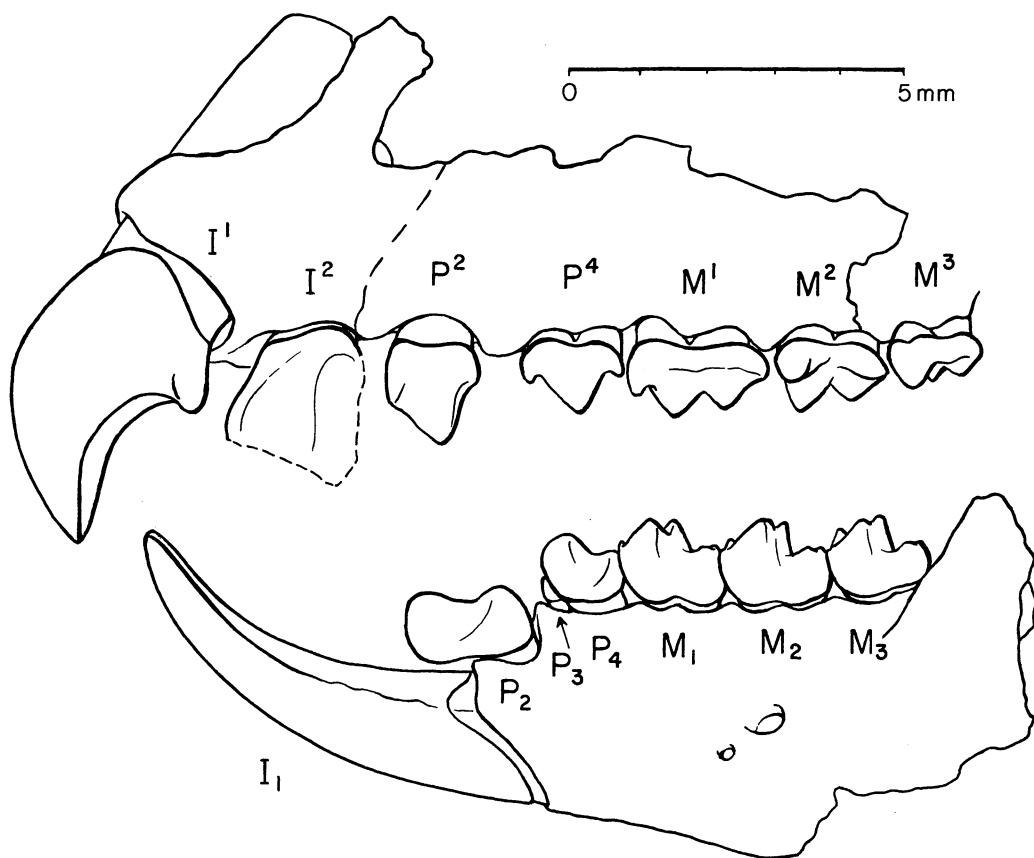
The type species of *Labidolemur* is *L. soricoides* from Mason Pocket, a late Paleocene (Tiffanian) locality in southern Colorado. *Labidolemur soricoides* was first described by Matthew and Granger (1921), based on two fragmentary lower jaws. *Labidolemur kayi* was later



TEXT-FIG. 2 — Lower dentition of *Labidolemur kayi* Simpson from Holly's Microsite (SC-188). Left dentary, UM 73500, in occlusal (A) and lateral view (B).

described by Simpson (1929) from Eagle Mine, a latest Paleocene (early Clarkforkian) locality near Bear Creek, Montana. The holotype of *L. kayi* (CM 11703) consists of a left mandibular ramus with P_4M_{1-3} . This specimen has a single-rooted P_4 , a well developed fossa below P_4 , and two large mental foramina below M_1 and M_2 , but no other diagnostic characteristics are preserved. Holly's Microsite (SC-188), source of the referred specimens of *L. kayi* described here, is slightly younger in age and situated about 30 km southeast of the Eagle Mine type locality (Gingerich et al., 1980, fig. 2).

Labidolemur kayi has had a checkered taxonomic history. Jepsen (1934) and Simpson (1935, 1940) retained *L. kayi* in the genus *Labidolemur*. McKenna (1960, 1963) transferred it to *Apatemys*, claiming that the holotype and referred specimens differ from *Apatemys bellus* only in having a short talonid on M_3 . West (1972) and most later authors accepted this transfer. West (1973) went so far as to synonymize *L. kayi* with *Apatemys bellus*. Russell et al. (1979) rejected West's synonymy at the species level and questioned placing *L. kayi* in *Apatemys*. Specimens described here are more complete than any previously available, and they indicate that *L. kayi* is more similar to *L. soricoides* than it is to *Apatemys bellus* in retaining P_3 as well as having a short talonid on M_3 . On the basis of this new evidence we return *L. kayi* to *Labidolemur*.



TEXT-FIG. 3 — Composite reconstruction of left upper and lower dentition of *Labidolemur kayi* Simpson in lateral view, based on specimens illustrated in Text-figures 1 and 2. Crown of P_4 restored from the holotype of *L. kayi* (CM 11703), and crown of M^3 restored from an early Wasatchian specimen from the Clark's Fork Basin (UM 66686).

Bown and Schankler (1982) questionably identified one Clarkforkian specimen (UM 68592, from SC-109) as *Apatemys chardini*. This specimen clearly differs from the holotype of *Apatemys chardini* in being larger and in retaining an alveolus for P_3 , and it is very similar to specimens of *Labidolemur kayi* (e.g., UM 73500, Text-fig. 2) in comparable parts. Hence we refer UM 68592 to *L. kayi*. *Labidolemur kayi* is the only species of Apatemyidae discovered to date in North American faunas of Clarkforkian age.

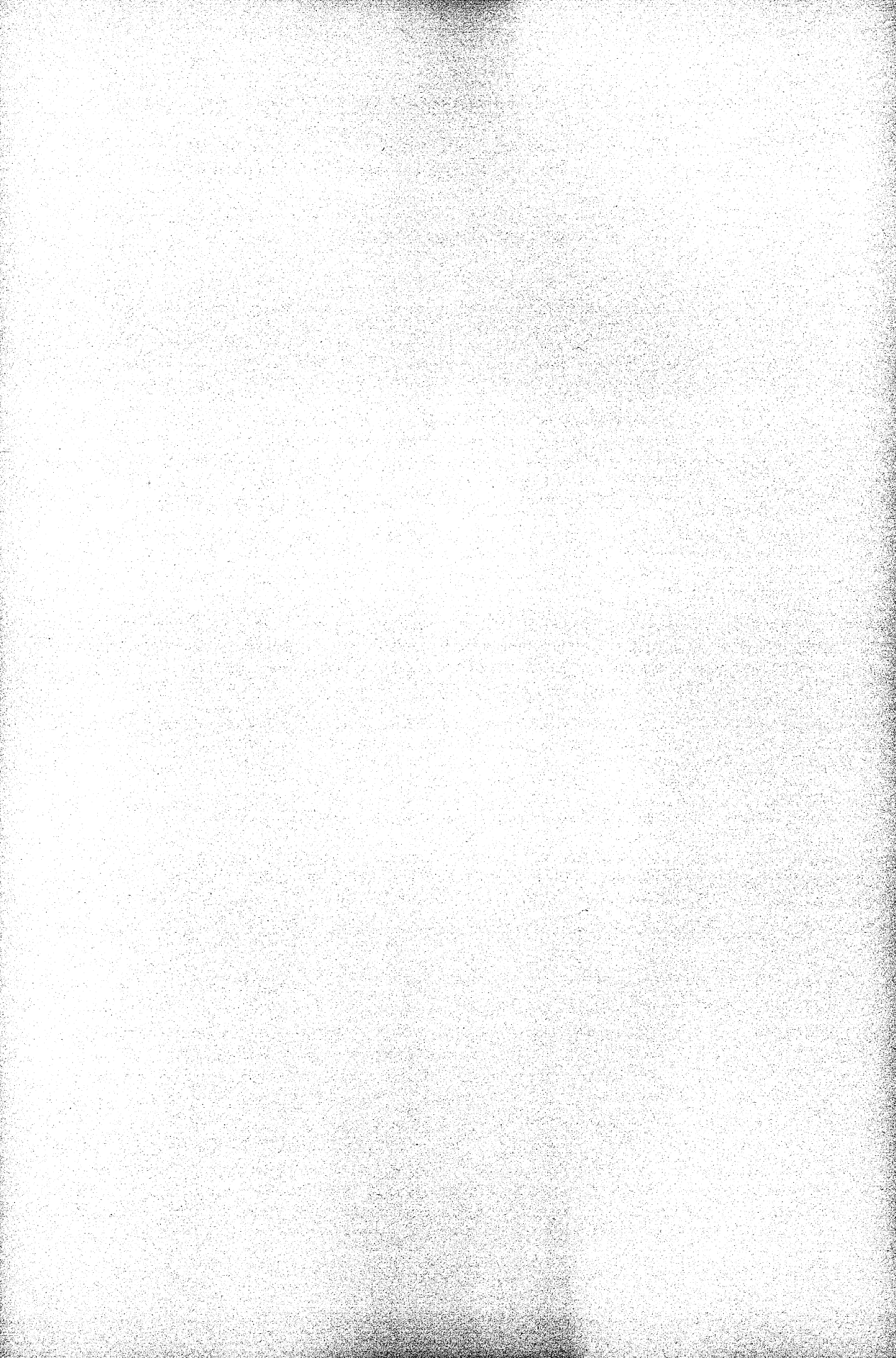
ACKNOWLEDGMENTS

We thank Dr. Mary Dawson, Carnegie Museum of Natural History, for loan of the holotype of *Labidolemur kayi*. We also thank Drs. Thomas M. Bown, David W. Krause, and David M. Schankler for reading the manuscript. University of Michigan specimens described here were prepared by Gerald Paulson and William Ryan. The drawings in Text-figures 1–3 are by Karen

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LABIDOLEMUR AND APATEMYS FROM THE EARLY WASATCHIAN OF THE CLARK'S FORK BASIN, WYOMING

BY

PHILIP D. GINGERICH

Abstract.—A single lineage of *Labidolemur* is known from the late Paleocene (Tiffanian Land-Mammal Age) of western North America. The middle Tiffanian species *L. soricoides* apparently gave rise to *L. kayi* in the late Tiffanian. *L. kayi* persists in the Clark's Fork Basin through the Clarkforkian and early Wasatchian Land-Mammal Ages. A second lineage of *Labidolemur*, represented by the new species *L. serus*, first appears following an interval of faunal turnover within the early Wasatchian, and it persists into the middle Wasatchian. *L. serus* is a sister species that probably evolved from *L. kayi*; however, intermediate forms are not yet known, suggesting that the transition occurred somewhere outside the Clark's Fork Basin. *Apatemys* (or *Teilhardella*) *chardini* is also known from the early Wasatchian of the Clark's Fork Basin. It differs from species of *Labidolemur* in having only two lower premolars (P_2 and P_4), and in having lower molars with relatively lower crowns. *Labidolemur* is an endemic North American genus, but *A. chardini* is similar to correlative or slightly older European species and it may represent an early Wasatchian immigrant from Europe.

INTRODUCTION

The systematic treatment of early Eocene species of Apatemyidae varies considerably. Apatemyids are known from many localities of the Wasatchian Land-Mammal Age in North America, but they are always rare faunal elements and they are usually represented by fragmentary specimens. In spite of a number of recent studies, the morphological variability of Wasatchian apatemyids is poorly documented. In the past seven years some 40 new specimens of Apatemyidae have been found in the Clark's Fork Basin of northwestern Wyoming. Most of these are early Wasatchian *Labidolemur kayi*, but a new species of *Labidolemur* (*L. serus*, see below) and several specimens of *Apatemys* (or *Teilhardella*) *chardini* are also represented. The primary objective of this paper is quantitative characterization of each of the three early Wasatchian species now known from the Clark's Fork and Bighorn Basins of northwestern Wyoming. Some incidental observations bearing on the phyletic history of Paleocene apatemyids are included in the discussion at the end of the paper.

The following museum acronyms are used in the text and figures: AMNH (American Museum of Natural History, New York), CM (Carnegie Museum of Natural History, Pittsburgh), PU (Princeton University Museum of Natural History, Princeton), UCMP (University of California Museum of Paleontology, Berkeley), UM (University of Michigan Museum of Paleontology, Ann Arbor), USGS-D (U. S. Geological Survey, Denver), UW (University of Wyoming

Museum of Geology, Laramie), and YPM (Yale Peabody Museum of Natural History, New Haven). Dental nomenclature is the same as that employed in the preceding paper (Gingerich and Rose, 1982). Numbered fossil localities prefaced by SC are from the Sand Coulee area of the Clark's Fork Basin, Wyoming. Detailed documentation of the Clark's Fork Basin localities and their stratigraphic relationships is on file at the University of Michigan (see also Gingerich et al., 1980; Rose, 1981; Gingerich, 1982).

DENTITION OF *LABIDOLEMUR KAYI*

Labidolemur kayi was first described by Simpson (1929) from Eagle Mine, a latest Paleocene (early Clarkforkian Land-Mammal Age) locality near Bear Creek, Montana. The holotype of *L. kayi* (CM 11703) consists of a fragmentary left mandibular ramus with P_4M_{1-3} . The ramus is broken in front of P_4 . The holotype has a single-rooted P_4 , a well developed fossa below P_4 , and two large mental foramina below M_1 and M_2 , but no other diagnostic characteristics are preserved. Our understanding of the dental morphology of this species is greatly improved following discovery of several exceptionally complete specimens from another Clarkforkian locality only 30 km southeast of the type locality (Gingerich and Rose, 1982). Known Wasatchian specimens of *Labidolemur kayi* do not differ significantly in tooth size or dental morphology from Clarkforkian specimens of this species.

Two specimens tentatively referred to *Labidolemur kayi* are known from latest Tiffanian age sediments in the Clark's Fork Basin (PU 19092, 20711), and eight specimens of this species are known from middle or late Clarkforkian localities (CM 11703, UM 68592, 71012, 71481, 73496, 73500, 73501, 73616). Most specimens of *L. kayi* come from localities of the early Wasatchian Land-Mammal Age in the Clark's Fork Basin-Polecat Bench area (UM 65150, 65187, 66686, 67040, 67380, 68486, 68565, 69979, 69980, 73013, 73135, 75951, 76641, 77399, 77449). Additional specimens of *L. kayi* from the Bighorn Basin (not studied) are present in the PU, USGS-D, UW, and YPM collections. Dental and mandibular variability in Clarkforkian and early Wasatchian *Labidolemur kayi* from the Clark's Fork Basin is summarized in Table 1.

NEW SPECIES OF *LABIDOLEMUR*

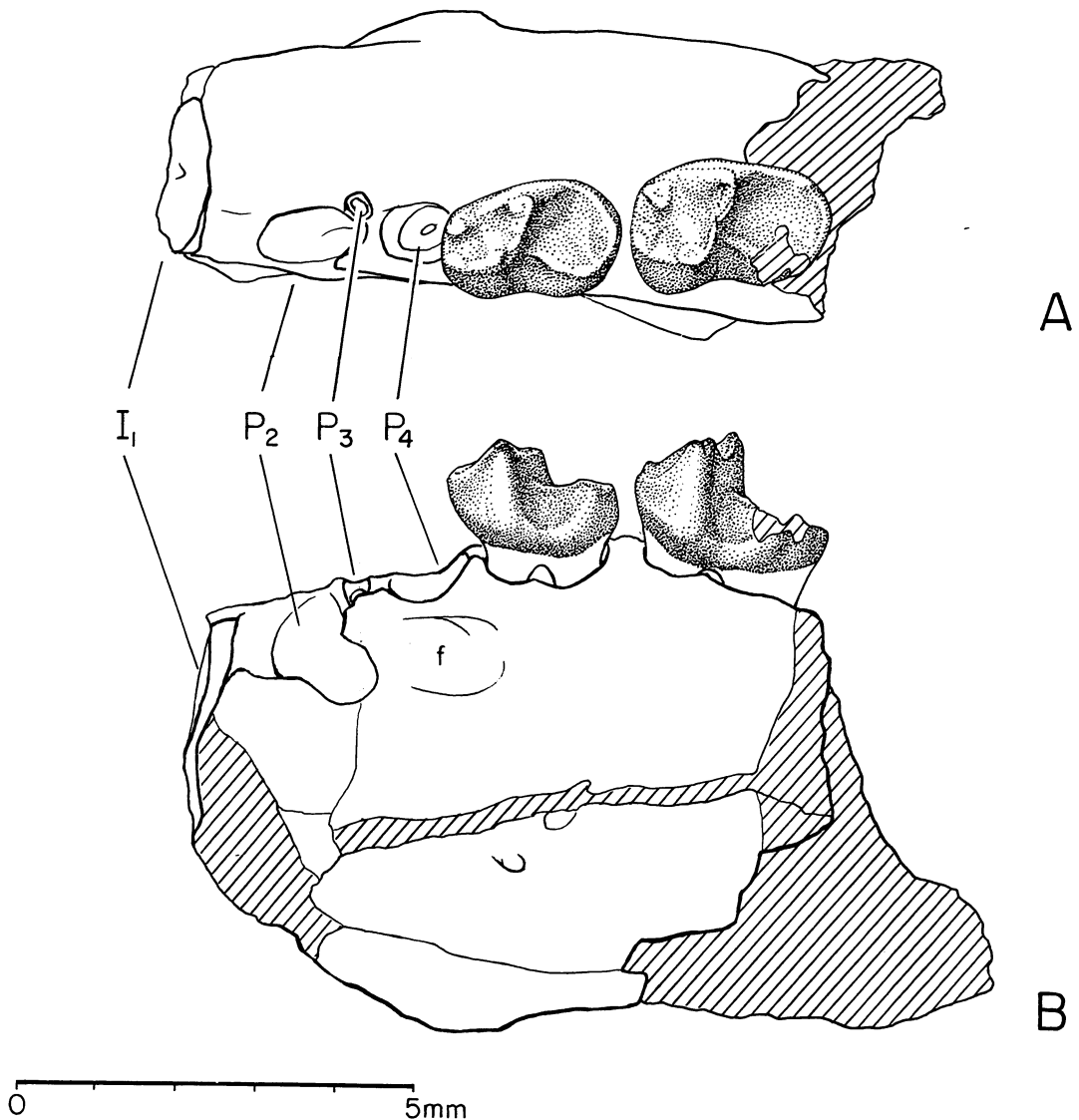
In addition to *Labidolemur kayi*, a larger species of *Labidolemur* is present in the early Wasatchian of the Clark's Fork Basin. This species is unknown below Schankler's (1980) "Biohorizon A," and it appears to be confined to the early and middle Graybullian faunal zones of the Wasatchian (upper *Haplomylus-Ectocion* Zone of Schankler).

***Labidolemur serus*, new species**

Holotype.—UM 69962, left dentary with root of I_1 , alveoli for P_{2-4} , and crowns of M_{1-2} (Text-fig. 1).

Type locality.—University of Michigan locality SC-128 in the Willwood Formation of the Clark's Fork Basin, center of $N \frac{1}{2}$, Sec. 30, T56N, R102W, Park County, Wyoming.

Age and distribution.—Early Wasatchian (early Eocene) of northwestern Wyoming. Locality SC-128 is at approximately the 2,100 m level in the principal Clark's Fork Basin stratigraphic section (see stratigraphic section in Gingerich, 1982). This locality produces a fauna of middle



TEXT-FIG. 1 — Holotype of *Labidolemur serus*, new species (UM 69962) from locality SC-128. Left dentary is drawn in occlusal (A) and lateral view (B). Note the depression or fossa (f) on the lateral side of the mandibular ramus below the alveolus for P_4 .

Graybullian age (early middle Wasatchian). *Labidolemur serus* is presently known only from the early and middle Wasatchian of the Clark's Fork Basin and central Bighorn Basin, Wyoming. One specimen, UCMP 44784, described by McKenna (1960) from Timberlake Quarry in the Sand Wash Basin of northern Colorado may also represent this species.

Hypodigm.—PU 18049, 18060, and UM 67038, 68588, 68590, 68591, 69129, 69132, 69962 (holotype), 71525, 73810, 73813, 73907, 73909 from the Clark's Fork Basin. YPM 22846 from Yale loc. 150 from the central Bighorn Basin.

TABLE 1 — Variability of tooth size and mandibular morphology in *Labidolemur kayi* Simpson of Clarkforkian and early Wasatchian age from the Clark's Fork Basin, Wyoming. *N* = sample size, *OR* = observed range, \bar{x} = mean, *s* = standard deviation, *V* = coefficient of variation. *L* = mesiodistal crown length, *W* = labiolingual crown width, and *H* = height at the base of the crown of *I*₁. Mandibular depth measured below *M*₂. All measurements in mm. Asterisk indicates an estimate.

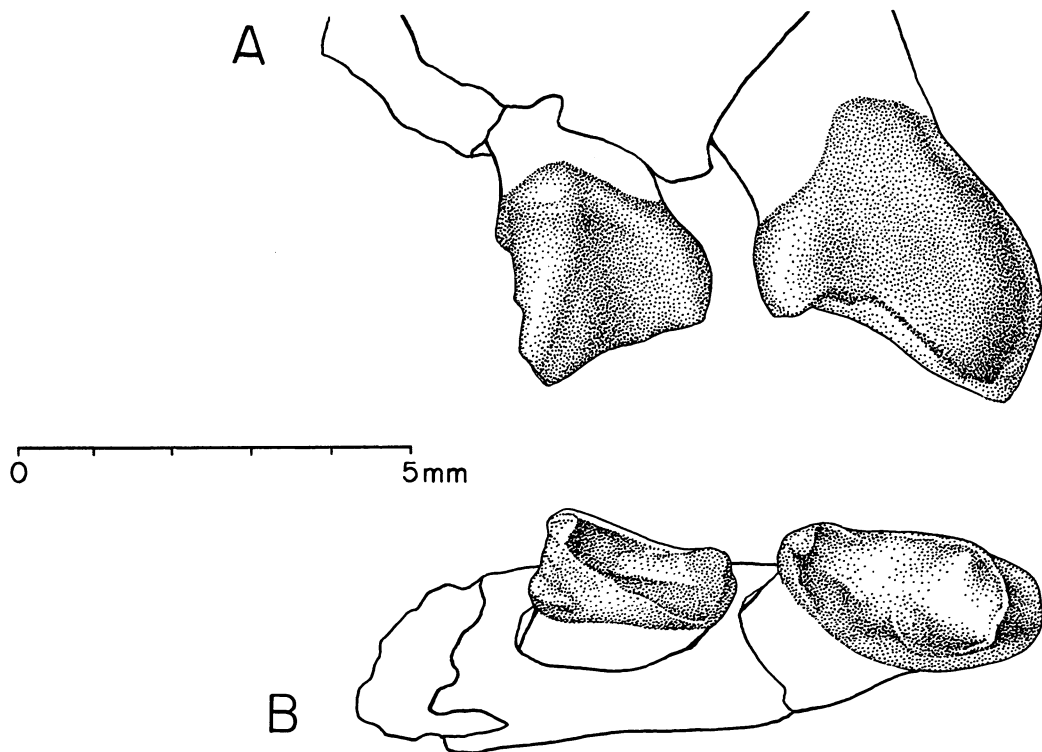
Tooth position		Holotype (CM 11703)	Clark's Fork Basin sample (excluding holotype)					
			<i>N</i>	<i>OR</i>	\bar{x}	<i>s</i>	<i>V</i>	
Maxillary dentition	<i>I</i> ¹	L	—	3	2.7–3.1	2.93	0.21	7.1
		W	—	3	1.2–1.5	1.37	0.15	11.2
	<i>I</i> ²	L	—	1	2.3*	—	—	—
		W	—	1	1.1*	—	—	—
	<i>P</i> ²	L	—	1	1.4	—	—	—
		W	—	1	0.6	—	—	—
	<i>P</i> ⁴	L	—	1	1.6	—	—	—
		W	—	1	1.2	—	—	—
	<i>M</i> ¹	L	—	1	2.1	—	—	—
		W	—	1	2.0	—	—	—
	<i>M</i> ²	L	—	2	1.9	1.90	—	—
		W	—	2	2.3–2.5	2.40	—	—
	<i>M</i> ³	L	—	1	1.5	—	—	—
		W	—	1	2.2	—	—	—
Mandibular dentition	<i>I</i> ₁	L	—	1	6.0	—	—	—
		W	—	10	1.3–1.7	1.56	0.12	7.5
		H	—	10	2.4–3.0	2.73	0.21	7.5
	<i>P</i> ₂	L	—	2	1.8–2.3	2.05	—	—
		W	—	3	0.9–1.1	1.00	0.10	10.0
	<i>P</i> ₃	L	—	1	0.3	—	—	—
		W	—	1	0.3	—	—	—
	<i>P</i> ₄	L	1.2	0	—	—	—	—
		W	0.8	0	—	—	—	—
	<i>M</i> ₁	L	1.8	5	1.7–1.9	1.80	0.10	5.6
		W	1.3	5	1.1–1.3	1.22	0.84	6.9
	<i>M</i> ₂	L	2.0	7	1.9–2.0	1.93	0.05	2.5
		W	1.7	7	1.4–1.5	1.43	0.05	3.4
	<i>M</i> ₃	L	1.9	4	1.7–1.9	1.83	0.10	5.2
		W	1.4	4	1.2–1.4	1.30	0.08	6.3
	Mand. depth		5.1	11	4.6–5.7	5.20	0.35	6.7
	Condition of <i>P</i> ₄ roots or alveoli		Single		Single: 9 (82%) Fused: 2 (18%) Double: 0 (0%)			
	Development of depression below <i>P</i> ₄		Large		Absent: 0 (0%) Slight: 3 (33%) Large: 6 (67%)			
Mental foramina		Double		Single: 1 (9%) Double: 8 (73%) Triple: 2 (18%)				

Etymology.—*serus*, L., late, in reference to the late appearance of this species in *Labidolemur* biochronology.

Diagnosis.—*Labidolemur serus* differs from *L. soricoides* and *L. kayi* in being about 15% larger in most linear dimensions. *L. serus* also differs from *L. soricoides* in having a relatively shorter premolar region with a smaller vestigial P_3 and, predominantly, a single-rooted P_4 (*L. soricoides* has a larger P_3 and double-rooted P_4 in all specimens at hand). *L. serus* also differs from *L. kayi* in having P_2 and P_4 closer together, in having a relatively higher crowned lower incisor, and in having a relatively deeper mandibular ramus (see discussion below).

Description.—*Labidolemur serus* differs from *L. kayi* in size but not in very many other morphological characteristics. The holotype of *L. serus*, UM 69962, is a left mandibular ramus preserving the root of I_1 , an alveolus for P_2 , a single root each for P_3 and P_4 , the intact crown of M_1 , and the slightly deformed crown of M_2 . There is a slight depression or fossa on the labial side of the dentary below P_4 , and there are two mental foramina. The holotype is illustrated in Text-figure 1, and dental measurements of this specimen are listed in Table 2.

A premaxilla of *Labidolemur serus* is known, UM 69129, preserving the crowns of I^{1-2} (Text-fig. 2). The anterocone on I^1 in this specimen shows heavy apical wear. Wear continues up the anterior surface of the anterocone in a way that could not have been caused by direct occlusion with I_1 . The posterocone of I^1 is also heavily worn on its lingual surface. A grooved wear facet indicates that the tip of I_1 sometimes occluded medially and just in front of the posterocone. The second incisor, I^2 , has an unusual pointed crown with a distinctively squared lateral profile. The



TEXT-FIG. 2 — Right premaxilla of *Labidolemur serus*, new species (UM 69129) from Hackberry Hollow (SC-192). A, lateral view, and B, occlusal view.

TABLE 2 — Variability of tooth size and mandibular morphology in *Labidolemur serus*, new species, of early Wasatchian age from the Clark's Fork Basin-Polecat Bench area, Wyoming. Abbreviations as in Table 1. All measurements in mm.

Tooth position	Holotype (UM 69962)	Clark's Fork Basin sample (including holotype)					
		N	OR	\bar{x}	s	V	
Maxillary dentition							
I ¹	L	—	1	3.5	—	—	—
	W	—	1	1.7	—	—	—
I ²	L	—	1	2.9	—	—	—
	W	—	1	1.5	—	—	—
P ²	L	—	1	1.8*	—	—	—
	W	—	1	1.0*	—	—	—
P ⁴	L	—	1	1.9*	—	—	—
	W	—	1	1.6*	—	—	—
M ¹	L	—	2	2.4	2.40	—	—
	W	—	2	2.3–2.4	2.35	—	—
M ²	L	—	2	2.1–2.2	2.15	—	—
	W	—	2	2.6–2.8	2.70	—	—
M ³	L	—	2	1.6–1.8	1.70	—	—
	W	—	2	3.0–3.1	3.05	—	—
Mandibular dentition							
I ₁	L	—	1	7.2	—	—	—
	W	1.9	9	1.7–2.1	1.89	0.15	8.1
	H	3.3	9	3.1–3.9	3.38	0.29	8.5
M ₁	L	2.2	3	2.0–2.2	2.10	0.10	4.8
	W	1.5	3	1.4–1.5	1.47	0.06	3.9
M ₂	L	2.4	4	2.1–2.4	2.23	0.13	5.7
	W	1.7	4	1.7–1.8	1.73	0.05	2.9
M ₃	L	—	1	2.2	—	—	—
	W	—	—	—	—	—	—
Mand. depth	—	—	4	6.2–6.9	6.60	0.32	4.8
Condition of P ₄ roots or alveoli	Single	Single: 5 (72%) Fused: 1 (14%) Double: 1 (14%)					
Development of depression below P ₄	Slight	Absent: 0 (0%) Slight: 4 (80%) Large: 1 (20%)					
Mental foramina	Double	Single: 1 (17%) Double: 5 (83%) Triple: 0 (0%)					



TEXT-FIG. 3 — Stereophotograph of maxillary dentition of *Labidolemur serus*, new species (UM 73907) from locality SC-34. Reproduced 3× natural size, scale bar = 1 cm.

apex of the principal cusp on I^2 is chipped slightly, and the complex occlusal surface anterior to this cusp is heavily worn from contact with the crown of I_1 .

The most complete maxillary dentition of *L. serus* is a palate, UM 73907, with right $P^{2,4}M^{1-3}$ and left M^{1-3} (Text-fig. 3). Upper cheek teeth of *L. serus* are larger but otherwise very similar to those of *L. kayi*.

Several dentaries of *Labidolemur serus* are known, and the lower dentition of this species is generally similar to that of *L. kayi*. Most teeth are larger, but, judging from the diameter of the alveolus (ca. 0.3 mm), P_3 was relatively smaller in *L. serus* than it is in *L. kayi*. P_2 and P_4 are closer together in *L. serus* than they are in *L. kayi*. The talonid of M_3 is relatively short, as is typical of the other species of *Labidolemur*.

Dental and mandibular variability in early Wasatchian *Labidolemur serus* from the Clark's Fork Basin is summarized in Table 2.

Discussion.—The holotype of *Labidolemur serus* contains only two molars in place, but these teeth are significantly larger than M_{1-2} in *L. kayi* and indicate that a distinct lineage is represented. The conformation of premolar alveoli, with an alveolus for P_3 consistently present, indicates that the genus represented is *Labidolemur* rather than *Apatemys*. One referred specimen, UM 78813, has a single-rooted alveolus for P_3 followed by alveoli for a double-rooted P_4 , ruling out the possibility that the root or alveolus here identified as that for P_3 could be an anterior root or alveolus for a double-rooted P_4 .

Comparing the entire Clark's Fork Basin sample of *Labidolemur serus* with that of *L. kayi* (Tables 1 and 2), upper and lower molars are about 15% larger in the former species. The crown height of the lower incisor is 24% greater and mandibular depth is 27% greater in *L. serus*. Six out of nine specimens have a relatively large depression below P_4 on the labial side of the mandible in *L. kayi*, whereas this depression is only slightly developed in four out of five *L. serus*. No specimens of *L. serus* have the crown of P_3 preserved but, judging from the diameter of the root, P_3 in *L. serus* was relatively smaller than P_3 in *L. kayi*. This suggests that P_3 was progressively reduced in the three successive species of *Labidolemur*.

DENTITION OF *APATEMYS CHARDINI*

A third lineage of Apatemyidae smaller than both *Labidolemur kayi* and *L. serus* is present in the early Wasatchian of the Clark's Fork Basin and the central and southern Bighorn Basin. The holotype of *Teilhardella chardini*, PU 13236, described by Jepsen (1930) from the early or middle Wasatchian of the central Bighorn Basin appears to belong to this lineage. *Teilhardella* has never been adequately diagnosed from *Apatemys*, and virtually all recent authors regard *Teilhardella* as a synonym of *Apatemys*. Three specimens of *Apatemys chardini* are known from the Clark's Fork Basin (UM 64934, 67310, and 76834), and these range through the early and early middle Wasatchian. *Apatemys chardini* is represented by eight specimens in the southern Bighorn Basin (UW 8997, 9571, 9630, 9632 [in part], 9634, 9725, 10415, and YPM 31170), all of early Wasatchian age. All specimens referred to *Apatemys chardini* by Bown and Schankler (1982) have been restudied and those not listed here represent *Labidolemur kayi* rather than *A. chardini*. *Apatemys chardini* appears to have been more common in the early Wasatchian of the southern Bighorn Basin than it was in the central Bighorn Basin or Clark's Fork Basin.

Dental and mandibular variability in the entire sample of *Apatemys chardini* from the Clark's Fork and Bighorn Basins is summarized in Table 3. *A. chardini* clearly differs from *Labidolemur kayi* and *L. serus* in being smaller and in lacking P₃. It also appears to differ in consistently having a double-rooted P₄ and a single mental foramen, but these characteristics are each known in only two specimens of *A. chardini*. In an attempt to further differentiate *A. chardini* from *L. kayi* and *L. serus*, relative crown height [RCH] of the lower molars was measured as shown in Text-figure 4A. The results are summarized in Table 4, which shows that *Apatemys chardini* has lower molars with significantly lower crowns at all three molar positions. This difference is illustrated graphically in Text-figure 4B,C, where the lateral profile of M₂ in *A. chardini* is compared with that in *L. kayi*. Comparative study of lateral profiles in other species of *Apatemys* may indicate whether *A. chardini* really belongs in *Apatemys* or if it should be retained in a distinct genus *Teilhardella*.

I have not compared the original specimens, but descriptions and measurements of UCMP 46167 from the Sand Wash Basin, Colorado, and AMNH 56310 from the Powder River Basin, Wyoming, given by McKenna (1960) and Delson (1971) match those of *A. chardini* most closely among early Wasatchian Apatemyidae.

DISCUSSION

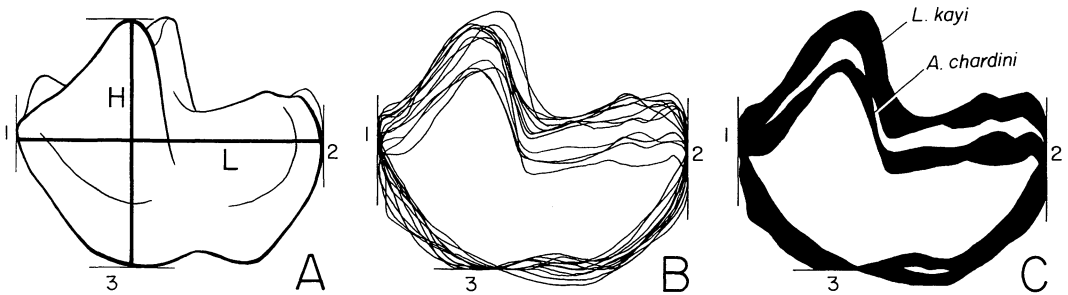
Tooth size and the lower dental formula are two of the most useful characteristics distinguishing genera and species of Paleocene and early Eocene apatemyids at present (Text-fig. 5). Tiffanian *Unuchinia* retains the greatest number of teeth in the lower dentition. It has a lower dental formula of 2.0.3.3, which is presumably the primitive formula for Apatemyidae. All other apatemyids differ in retaining only one lower incisor. Torrejonian *Jepsenella* and Tiffanian *Labidolemur* both have lower dental formulae of 1.0.3.3, and these genera may represent successive stages of a single lineage. Tiffanian "*Jepsenella*" *major* has a dental formula of 1.0.3.3 as well, but its phyletic relationships and generic allocation are problematical (see discussion in Russell et al., 1979, p. 206). *Labidolemur kayi* is the only apatemyid species known from the Clarkforkian. Three lineages of Apatemyidae are present in the early Wasatchian of the Clark's Fork Basin, and one of these, *A. chardini*, has the reduced dental formula characteristic of later *Apatemys*.

TABLE 3 — Variability of tooth size and mandibular morphology in *Apatemys chardini* from the Clark's Fork and Bighorn Basins, Wyoming. Abbreviations as in Table 1. All measurements in mm.

Tooth position	Holotype (PU 13236)		Clark's Fork and Bighorn Basin samples (including holotype)					
			N	OR	\bar{x}	s	V	
Maxillary dentition								
M ¹	L	—	1	1.8	—	—	—	—
	W	—	1	1.6	—	—	—	—
M ²	L	—	1	1.7	—	—	—	—
	W	—	1	1.9	—	—	—	—
Mandibular dentition								
I ₁	L	—	—	—	—	—	—	—
	W	1.1	2	1.1	1.10	—	—	—
	H	2.0	2	2.0–2.2	2.10	—	—	—
P ₂	L	—	—	—	—	—	—	—
	W	0.5	1	0.5	—	—	—	—
P ₄	L	1.0	1	1.0	—	—	—	—
	W	0.6	1	0.6	—	—	—	—
M ₁	L	—	2	1.6	—	—	—	—
	W	—	2	1.1	—	—	—	—
M ₂	L	—	6	1.7–1.8	1.75	0.05	3.1	—
	W	—	6	1.1–1.3	1.20	0.06	5.3	—
M ₃	L	1.7	1	1.7	—	—	—	—
	W	1.1	1	1.1	—	—	—	—
Mand. depth		4.0	1	4.0	—	—	—	—
Condition of P ₄ roots or alveoli		Double		Single: 0 (0%) Fused: 0 (0%) Double: 2 (100%)				
Development of depression below P ₄		Large		Absent: 0 (0%) Slight: 0 (0%) Large: 2 (100%)				
Mental foramina		Single		Single: 2 (100%) Double: 0 (0%) Triple: 0 (0%)				

Labidolemur kayi probably evolved from *L. soricoides* in the late Tiffanian, and in the Clark's Fork Basin it persisted through the Clarkforkian and early middle Wasatchian. *Apatemys chardini* first appeared at the beginning of the Wasatchian. *Labidolemur serus* first appeared following the "Biohorizon A" faunal turnover of Schankler (1980), i.e., in the middle of the early Wasatchian. The origin of the *A. chardini* and *L. serus* lineages is unknown, but both appeared following episodes of faunal turnover and both are plausibly regarded as immigrants into the Clark's Fork Basin-Polecat Bench area.

The beginning of the Wasatchian Land-Mammal Age in North America is marked by



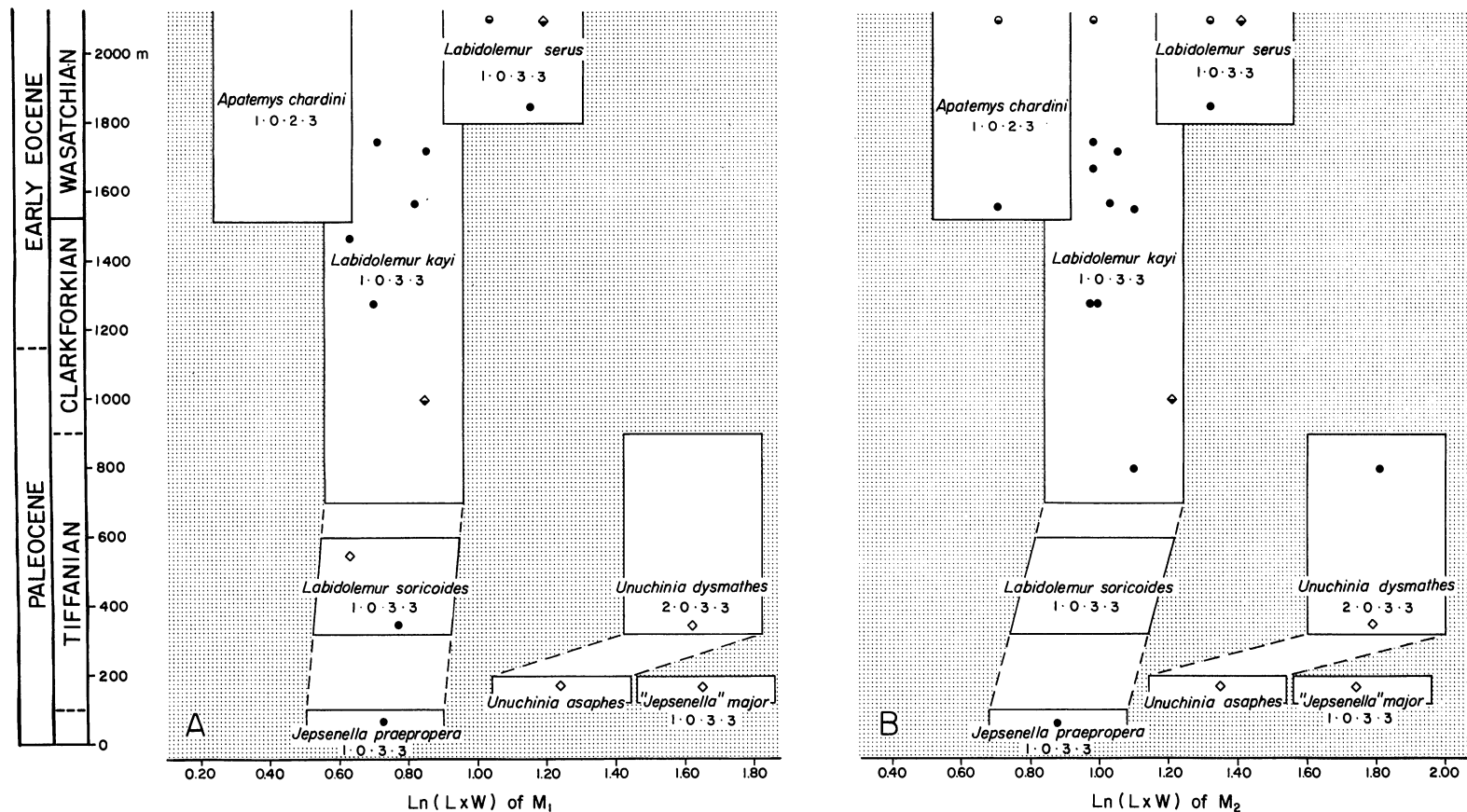
TEXT-FIG. 4 — Lateral profile of M_2 in *Labidolemur kayi* and *Apatemys* (or *Teilhardella*) *chardini*. A, left M_2 in lateral view, showing points of orientation and standardization for subsequent drawings. Metaconid omitted from all lateral profiles. All outlines brought to standard length at points 1 and 2, and then standard height at point 3 (relative crown height, RCH, measured as H/L ; see Table 4). B, standardized lateral profiles for eight specimens of *L. kayi* and four specimens of *A. chardini*. C, lateral profiles shaded to show distinct patterns of variation characteristic of each species. *L. kayi* has a higher trigonid and talonid than *A. chardini*. Oriented as shown here, the base of the crown below the hypoconid in *L. kayi* is approximately level with that below the protoconid, but the base of the crown below the hypoconid in *A. chardini* is relatively lower.

immigration of several important groups of mammals, including the first representatives of Artiodactyla, Perissodactyla, hyaenodontid Creodonta, and tarsiiform and lemuriform Primates (Rose, 1981). All of these appear to have had precursors in the early Sparnacian (earliest Eocene) of Europe, suggesting that they may have immigrated as one integrated faunal cohort to North America via Europe (Gingerich, 1980; Godinot, 1981). Earlier representatives of these groups are unknown in Europe and their center of origin is also unknown. *Apatemys chardini* may have immigrated into North America from Europe as part of this Wasatchian faunal cohort. Apatemyidae are not known with certainty from the Paleocene of Europe, but the presence of three species referred to *Apatemys* and a total of four or possibly five lineages of apatemyids in the early Sparnacian (Russell et al., 1979) suggests that Europe may have been closer than North America to the center of origin of *Apatemys chardini*.

TABLE 4 — Relative crown height [RCH] in Clarkforkian and early Wasatchian *Labidolemur* and *Apatemys* from the Clark's Fork and Bighorn Basins. RCH is measured as protoconid height above base of crown at anterior root/ anteroposterior crown length (measured on unworn or little worn teeth only; see Text-fig. 4). Asterisk indicates that differences are statistically significant at $p < 0.05$. Other abbreviations as in Table 1.

Tooth position	Genus and species	N	OR	\bar{x}	s
M_1	<i>Apatemys chardini</i>	2	0.63–0.69	0.660*	0.042
	<i>Labidolemur kayi</i>	6	0.71–0.82	0.762	0.044
	<i>Labidolemur serus</i>	2	0.76–0.80	0.780	0.027
M_2	<i>Apatemys chardini</i>	4	0.59–0.67	0.630*	0.037
	<i>Labidolemur kayi</i>	8	0.74–0.89	0.775	0.052
	<i>Labidolemur serus</i>	2	0.77	0.770	—
M_3	<i>Apatemys chardini</i>	1	0.59	0.59*	—
	<i>Labidolemur kayi</i>	5	0.63–0.68	0.664	0.023
	<i>Labidolemur serus</i>	1	0.68	0.68	—

CLARK'S FORK BASIN-POLECAT BENCH APATEMYIDAE



TEXT-FIG. 5 — Stratigraphic distribution of Paleocene and early Eocene Apatemyidae in the Clark's Fork Basin-Polecat Bench area. Abscissa is tooth size for M₁ and M₂, respectively. Ordinate is stratigraphic level above the Cretaceous-Paleocene boundary. Each circle represents one specimen. Diamonds represent type specimens. Solid figures are from measured stratigraphic levels in the Clark's Fork Basin-Polecat Bench area. Half solid figures are positioned vertically based on faunal correlations within the Clark's Fork Basin. Open figures are type specimens from other basins in the Western Interior of North America. Note that *Apatemys* (or *Teilhardella*) *chardini* first appeared at the beginning of the Wasatchian Land-Mammal Age, and *Labidolemur serus* appears at about the level of Schankler's (1980) "Biohorizon A."

Apatemys differs from *Labidolemur* and other Paleocene apatemyids principally in having a reduced dental formula (1.0.2.3). *Apatemys*, as presently conceived (including *A. chardini*), may be polyphyletic. One or more late Wasatchian species placed in *Apatemys* could be descendants of *Labidolemur* that lost vestigial P₃ and thereby independently gained a reduced dental formula. Relative crown height values are consistently higher in *Labidolemur kayi* and *L. serus* than they are in *Apatemys chardini* (Table 4), and relative crown height could prove to be important in distinguishing genera and species of Apatemyidae.

The one specimen of *Jepsenella praepropera* available, PU 19184, has lower molars (M₁ and M₂) with relative crown height [RCH] values of 0.94, and the holotype of "*Jepsenella*" *major* (AMNH 88343) has M₁ and M₂ RCH values of 0.81. One specimen of *Unuchinia dysmathes* (PU uncatalogued) has an M₂ RCH value of 0.96. *Labidolemur soricoides* (UM 64517) has an M₁ RCH value of 0.72. Thus it appears that *Unuchinia* probably retains primitively high crowned cheek teeth. Primitively high RCH values became reduced to about 0.70–0.80 in Tiffanian, Clarkforkian, and early Wasatchian species of *Labidolemur*. RCH values in *Apatemys chardini* range from about 0.60 to 0.70.

Two middle and late Wasatchian specimens referred to *Apatemys bellulus* (UM 66092) and *Apatemys* cf. *rodens* (USGS-D 3928) by Bown and Schankler (1982, and pers. comm.) have RCH values of 0.76. Thus they resemble *Labidolemur* more closely than they do *Apatemys chardini*. This could be interpreted to mean that late Wasatchian species of *Apatemys* are descendants of *Labidolemur*, in which case the dental formula of 1.0.2.3 in low crowned "*A.*" *chardini* evolved independently and this species should probably be placed in the separate genus *Teilhardella*. Alternatively, it may mean that high crowned *Labidolemur*-like cheek teeth in late Wasatchian *Apatemys* evolved independently from a low crowned *A. chardini*-like ancestor. More detailed study of middle and late Wasatchian *Apatemys* will be required to distinguish between these two possibilities.

Judging from casts and photographs, early Eocene apatemyids from Europe described by Russell et al. (1979) and referred to *Apatemys* are also low crowned. If *Apatemys* and *Teilhardella* do prove to be distinct, the European species probably represent *Teilhardella* rather than *Apatemys*.

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